

3.—Species diversity in the southwestern flora

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Abstract

The South West Botanical Province is noted for its floristic richness and high degree of endemism. Over 30% of the total species of *Epacridaceae*, *Myrtaceae* and *Proteaceae* are recorded in the Province. The percentage of species restricted to the area, calculated from available data, is 68%.

The flora is clearly related to that of eastern Australia with only tenuous links with the flora of South Africa and Malagasy.

The richness has arisen through the relative isolation of the area, major climatic fluctuations, and the diversification of the flora on sandy and gravelly soils with a marked summer drought.

Introduction

The South West Botanical Province of Western Australia is the southwestern corner of the State, where there is a reliable winter rainfall and marked summer drought. The boundary has been variously defined by Diels (1906) and Gardner (1942; 1956) as a line extending from Shark Bay (latitude 26° S, longitude 114° W) in the north to Israelite Bay (latitude 33° S, longitude 124°) in the south. The crescentic area west of this boundary is approximately two hundred thousand square kilometres.

Nowhere is the boundary between the South West Province and the Eremaean Province well-defined. Gardner (1942) relied upon a 175 mm winter (May to October) isohyet to substantiate his field observations on the distribution of what he considered South-Western and Eremaean species. Diels (1906) used the 300 mm annual isohyet, a line slightly to the west of Gardner's. Burbidge (1960) also accepted this line, using the 10" isohyet. These are presented in Figure 1.

Floristically the South West Province is delimited by the inland extent of many heath components such as *Conostylis*, *Anigozanthos* (*Haemodoraceae*) and the *Restionaceae* and *Epacridaceae*. The eastern limits of low heaths on sand or gravel, mallee and mallee heaths and certain woodlands also delimit the South West Province. Further east are the Mulga, Salmon Gum woodlands and shrublands dominated by species of *Acacia* and species of *Chenopodiaceae* and *Myoporaceae*.

Floristic diversity

Few studies have been made on the lower plants of Western Australia. Bibby and Smith (1954) list 36 lichens for the whole state and an estimate of the numbers of Bryophytes can only be made from a few localised studies.

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Smith (1962) lists the number of Bryophytes on granitic slopes in the well-watered Porongurup Range as 14. Willis (1954) has listed some 33 mosses, 20 of which occur in the dry Goldfields region.

The number of ferns and fern allies for Western Australia is only 49 (Smith, 1966). Of these, 26 occur in the South West Province, most being associated with moist microhabitats on granitic monadnocks. To this list must be added five or six south-west species of *Isoetes*.

Only 11 Gymnosperms are recorded for the province. This includes one widespread *Macrozamia*, a shrubby species of *Podocarpus* with morphological affinities with the eastern species *P. spinulosus* (Dallimore and Jackson, 1966) and six species of *Callitris* as well as three species of the endemic *Actinostrobus*.

Beard (1969) records a total of 3,611 Gymnosperms and Angiosperms in the South West Province. This record was based on data, extracted from species folders in the W.A. Herbarium, which were published as a "Descriptive Catalogue of West Australian Plants" (Beard, 1965). These data are limited because so much of the Western Australian flora still remains to be studied.

In comparison with most parts of the world the recorded number of ferns, Gymnosperms and Angiosperms in the South West Province is relatively high, though a survey of recent literature reveals other areas which have greater numbers of species per square kilometre. These data are presented in Table 1, arranged in decreasing species density. Species numbers have been obtained from Adamson and Salter (1950), Allan (1961), Beadle *et al.* (1972), Black (1929), Burbidge and Gray (1970), Chippendale (1971), Curtis (1969) and Willis (1962).

Table 1

The numbers of plant species in the floras of different regions

	Area sq. km	Estimated no. of species	Species per sq. km
Cape Peninsula, South Africa ..	471	2,622	5.567
Australian Capital Territory	2 359	1,037	0.440
Sydney District	28 500	2,000	0.070
Tasmania	68 330	1,200	0.018
South West Province	220 150	3,637	0.017
Victoria	227 620	2,500	0.011
New Zealand	268 670	1,457	0.005
South Australia	984 380	2,500	0.003
Northern Territory	1 347 525	2,736	0.002

The incredible diversity of the Cape Peninsula flora is no doubt partly due to its diverse

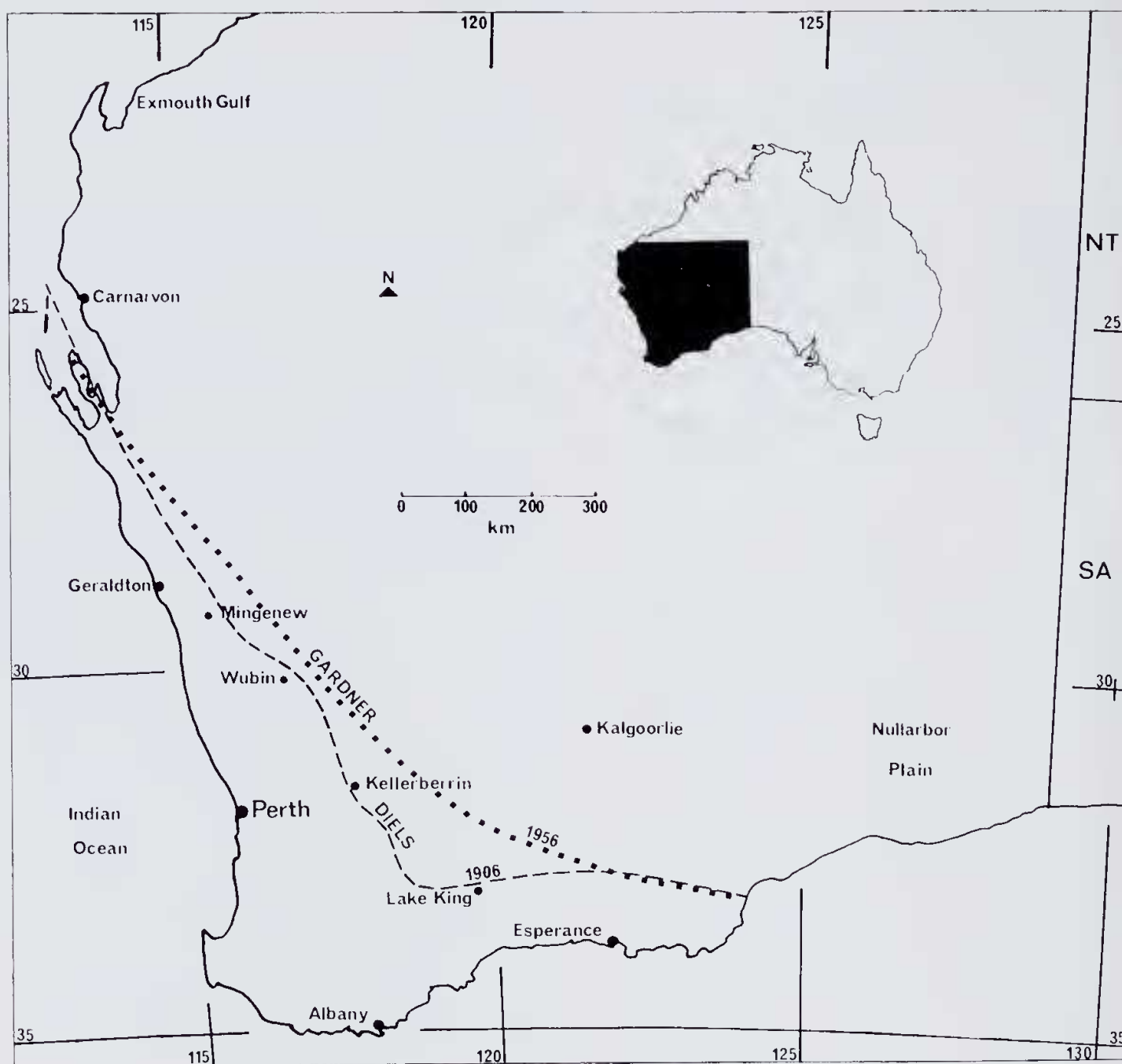


Figure 1.—The South West Botanical Province as defined by Diels (1906) and Gardner (1956).

physical features, which modify the climate so that various locations receive from 50 to over 200 cm annual rainfall. The higher elevations also receive summer mists, which must alleviate the summer drought to some extent. Of the species total recorded by Adamson and Salter (1950), 846 are monocots. In comparison, Beard (1965) lists less than 700 monocots for the South West Province, a lower proportion than that of the Cape Peninsula, due to the absence of many bulbous plants in the former.

In comparison to the data available on the number of species in other Australian states the South West Province compares favourably. The richness of the flora and its high degree of endemic species have been commented on by

many authors. Burbidge (1960) in a detailed analysis of Australian genera listed 462 genera in 96 families in the South West province. Of this total 111 genera are restricted to the Province. Only five families are endemic. These are Cephalotaceae, (1 sp.); Eremosynaceae, (1 sp.); Emblingiaceae, (1 sp.); Ecdeiocolaceae, (1 sp.); Anarthriaceae, (5 spp.). The last two families are morphologically and anatomically related to the Restionaceae but are regarded as separate families by Cutler and Airy Shaw (1965).

Among the families which are well represented by a number of genera in the province are the Restionaceae (16 genera), Liliaceae (21), Xanthorrhoeaceae (9), Myrtaceae (26), Epacridaceae (15), Leguminosae (31), Rutaceae (13).

Goodeniaceae (10) and Asteraceae (30) (largely from Burbidge, 1960).

At the species level, Gardner (1942) lists the families well developed in the province as Tremandraceae, Proteaceae, Leguminosae, Rutaceae, Rhamnaceae and Verbenaceae.

An indication of the number of species in some of the larger families of the province and the percentage of the total species estimated for Australia is presented in Table 2. Data have been extracted from Burbidge (1963) and Beard (1965).

Table 2

The numbers of species in selected families of plants from the South West Province and the whole of Australia

	Estimated total Australian species	Estimated S.W. province species	Percent. of Australian species in S.W.
Centrolepidaceae	35	23	66
Dilleniaceae	107	63	59
Epacridaceae	499	170	34
Goodeniaceae	309	128	41
Myrtaceae	1,918	603	32
Proteaceae	1,211	408	34
Restionaceae	82	57	70
Stylidiaceae	144	102	71

The three large families Epacridaceae, Myrtaceae and Proteaceae, which are regarded by Good (1964) as large Australian families, have between them over 3,600 species, over one-third of the total number of species in the Australian flora estimated by Good (*loc. cit.*). The South West Province total of these three families is just under 1,200 species, which is one third of the total number of species of the families and one third of the species total of all families recorded for the province.

In contrast to the richness in the south-west of the families presented in Table 2 are the distribution patterns of the other large Australian families listed by Good (*loc. cit.*). For example in the Poaceae, Gardner (1952) records only 82 species native to the Province in comparison to 278 native Western Australian grasses. Figures for the Orchidaceae (George, 1971) reveal the same degree of paucity in the South West Province, only 128 species out of an Australian total of approximately 600. The numbers of species of Australia's largest genera *Acacia* and *Eucalyptus* show the same pattern. Only 161 *Acacia* species are recorded and 79 eucalypts out of a total of very approximately 600 species for each genus. The southwestern representatives of the two genera respectively contribute only 27% and 13% of the Australian total.

Endemism

Good (1964) comments on the difficulties in comparing species richness and degrees of endemism. No attempt will be made here to present the facts using the methods outlined by Exell and Williams (*vide* Good *loc. cit.*).

The high degree of endemism in the flora of southwestern Australia has been commented on by Hooker (1860), East (1912) and Gardner (1942; 1959). The number of species restricted to the South West Province has been estimated at 75% of the southwestern flora (Gardner, 1959) and as 86-87% by Beard (1969). The latter paper, based on the descriptive catalogue mentioned above (Beard, 1965), and a survey of the literature, presents figures for the number of both widespread and restricted species for the South West Province, the Eremaean Province and the Northern Province. The percentages of endemism recorded in the analysis are not clearly comprehensible, as there is some confusion between the use of the terms "endemic" and "solely southwestern" as well as errors in calculation. On the basis of figures listed by Beard, the number of species restricted to the South West Province is 2,472 and the total number of species in the province is 3,611. This means that the percentage of species restricted to the province is 68%.

In comparison with this percentage of endemism Good (1964) suggests that the Cape Peninsula, South Africa, has more than 90% endemism. Malagasy is also quoted as perhaps having 85% of the species being restricted to the island. It must be remembered however that the larger an area the higher the proportion of endemic species. Australia for example probably has a greater proportion of endemic species than any other major geographical region.

Figures for species endemism also exist for Tasmania (Curtis 1969) as 17% and for Darwin and the Gulf region of the Northern Territory, 57% (Chippendale 1971), though this latter figure apparently refers only to the percentage of endemism of that region in comparison to the Northern Territory and not the neighboring States.

There is no doubt that the South West Province does have a high degree of endemism in comparison to other regions of comparable size. It is also worth noting that a considerable area of the South West Province is covered by forests and woodlands which are dominated by a single or very few species of *Eucalyptus*. For example, prime forests of Jarrah (*Eucalyptus marginata* Donn ex Sm.) cover over 17,000 sq. km yet harbour only a few hundred associated species. The incredible richness and uniqueness of the local flora is to be found on the heaths or so called sandplains of sandy or lateritic soil which occupy considerable areas, particularly in the northern and eastern parts of the province. Diels (1906) and Gardner (1942) comment on this richness at the "cusps" of the province. Diels (*loc. cit.*) quotes the total number of recorded species and the percentage endemism in each of the six botanical districts he designated within the Province. Even though his total figures are low and it is not clear if he uses the term "endemism" to refer to the species restricted to the district or whole Province, the results are interesting. Endemism is quoted as 6% for the extreme south-west corner, 37% for the most

northerly district and 33% for the most easterly. The districts in between range from 20 to 33%.

An indication of the species richness of heath areas of the province is given in Table 3, which presents recent information on the species total in three reserves.

Table 3

The numbers of species in selected National Parks in southwestern Australia

	Area (sq. km.)	No. of species
Tutanning (32° 30'S, 117°E.)	18.2	400
Stirling Range (34°S, 118°E.)	1 093	550
Fitzgerald River (32° 30'S, 117°E.)	2 444	700

With more field work the figures for the species of the Stirling Range and Fitzgerald River reserve will rise. Already it has been found that 10% of the plants of the Fitzgerald River reserve are restricted to that area. Most of these local endemics are restricted to the slopes of the Barren and Eyre Ranges which rise to over 500 m. It is worth noting from the above data that the species density of Tutanning, the most intensively studied reserve, is 22 species per square kilometre. This figure is probably typical of many small areas of heath in the south-west, particularly along the southern coast on some monadnocks such as Mt. Manypeaks and Peak Charles and some mountain ranges such as the Stirling Range, the Barrens and Mt. Ragged. A similar situation exists in the Grampians, Victoria, with approximately 750 species of angiosperms and ferns, 30 of them restricted to that location in Victoria and some of these having Western Australian affinity (Willis, 1962).

Disjunctions and links with other floras.

The closest relationship of the South West Province judging by the number of shared genera and species is with southeastern Australia. Beard (1969) records 491 species which occur in the south-west and in eastern Australia. Of these 211 are widespread in Western Australia while 280 are restricted in Western Australia to the South West Province and also occur in the south-east of Australia.

Green (1964) mentions that several hundred species occur in the south-west and in the eastern states but not in the intervening regions of Western Australia and western South Australia. He selected 35 of these with a minimum intervening distance in their distribution of 1200 km and a maximum of 2500 km. A recent unverified collection of the species quoted with the greater disjunction, (*Stylidium perpusillum* Hook f.), reduces the intervening distance to 1600 km. In the same paper, Green lists 48 pairs of species, the members of which are regarded as morphologically related and far removed geographically. Some of these are considered by Green to be true vicariads which

have been separated by unfavourable climatic conditions in the intervening region and have diverged morphologically.

The explanation for some of the disjunct species listed by Green is regarded as long distance wind dispersal. To support this suggestion the author refers to the high proportion of minute-seeded species such as Orchidaceae, *Stylidium* and *Levenhookia* in his lists. Recent work on the Orchidaceae at the Western Australian Herbarium has revealed other species which could be added to list of southwestern and southeastern Australian species. One of these, *Thelymitra mathewsii* Cheeseman, occurs in a few localities at the northern tip of New Zealand (George, 1971). This is only a few degrees of latitude south of the Western Australian occurrence, and approximately 5000 km to the east.

Disjunctions between southwestern and south-eastern Australian species with large propagules require an explanation involving geological and climatic history. Disjunctions within the South West Province itself, particularly between the northern and southeastern sections and between the south-west and the granitic monadnocks of the interior, can also be explained on the basis of past climatic fluctuations. This subject will be dealt with later.

A floristic relationship between southern and east Africa and Western Australia is often quoted in the literature on plant geography and continental drift. This relationship has been discussed by Gardner (1942), Specht (1958), Burbidge (1960) and Good (1964). Specht *loc. cit.*, lists four genera which range from East Africa and Malagasy to Australia. These are *Adansonia*, *Diplopeltis*, *Keraudrenia* and *Rulingia*. These genera except *Adansonia* are well represented in the South West Province. The record for *Diplopeltis* from Malagasy has recently been refuted (George and Erdtman, 1969) though Hoogland (1949) adds the genus *Hibbertia*, which is very well represented in the south-west, to those genera which occur in Malagasy and Australia.

Gardner (1942) and Burbidge (1960) discuss in detail the distribution of the families Centropolepidaceae, Restionaceae and Proteaceae and their links between southwestern Australia, southern Africa and southern South America. These links are well developed only at the family level. Weimarck (1941) listed only four genera which occur in the Cape Peninsula and in the South West Province. These are *Restio*, *Leptocarpus* and *Hypolaena* (Restionaceae) and *Caesia* (Liliaceae). As pointed out by Burbidge (1960) there is no certainty that the respective taxa in the two regions are congeneric. Certainly very little is known at the present time of the generic limits within the local Restionaceae.

The case of the distribution of the Proteaceae is frequently regarded as a keystone in phytogeographical interpretation, rivalling the position of Nothofagus. The study of the distribution of genera (Rao, 1971) reveals that none of those represented in Western Australia occur

outside Australia and that there is a greater relationship between Australia and South America than between South Africa and Australia.

The concept of a close relationship between the flora of southern South Africa and the South West Province has arisen largely because of the incredible morphological similarity of some genera, particularly in Proteaceae and Papilionaceae, in the respective regions. This similarity, as well as the parallel floristic diversity and localised richness of the two areas, suggests not recent contact but a parallel in environmental history.

Thus the relationships of the southwestern flora are clearly with that of eastern Australia and, in common with that region, the northern regions of Australia and the neighbouring islands. Through the relationship of the flora of eastern Australia to that of New Guinea, New Caledonia, New Zealand and South America, the western flora is more related to these as well, than it is to that of southern Africa and Malagasy.

Discussion

A considerable amount of controversy has raged over the location of the origin of the angiosperms. The most widely accepted view at present is that they arose in the area which now lies between Assam and Fiji, most probably in what is now south-east Asia (Takhtajan, 1969).

Hooker (1860) suggested that the South West Province was a cradle of angiosperm development but later workers such as Crocker and Wood (1947) dispute this, pointing out that the area is merely a centre of diversity. The figures presented earlier showed this diversity in some of the families represented in the south-west. Cytological evidence on the origin of the Myrtaceae and Epacridaceae (Smith-White, 1959) points to an eastern Australian origin for most of the genera within these families. Rao (1971) also suggests an eastern origin for the Proteaceae. Thus the South West Province is only a centre of diversity in a few families which are usually considered as typical "Australian elements". The origin of the Australian flora then, lies either in the eastern Australian region or, as is probably more likely, in the area to the north of that region.

Smith-White (1959) believes that the angiosperms developed outside Australia and that the orders and families were established before the predicted massive invasion of Australia after the mid-Cretaceous. Beadle (1966) also follows this view.

It is significant to note that the suggested period of the drifting apart of the pre-Cretaceous great southern continent was the Neocomian, the same period as that of the earliest fully-authenticated Angiosperm remains (Takhtajan, 1969). It is possible that the flowering plants were well developed at the time of this separation but it is doubtful if many present day families had appeared. Thus the very

tenuous botanical relationship between the South West Province and Africa could possibly be due to continental drift. As well, if we accept that the final breaking up of the southern continental mass into Australia, Antarctica and South America occurred at a much later date then we would expect the greater degree of botanical relationship between Australia and South America, as has been found.

Burbidge (1960) discusses the affinities of the floras of the southern continents, pointing out that the reconstruction of "Pangaea" by Carey (1958) fails to explain the strong generic affinities between South America and Australia and the lack of them with South Africa. More recent reconstructions of the supposed southern continent by Griffiths (1972) and the paper dealing with geological history in this volume, show how it is possible for Australia to have more affinities with South America than South Africa. However it must be pointed out again that Africa is supposed to have separated from "Gondwanaland" before most modern plant families had appeared.

Far more important considerations than continental drift and links with other floras are those dealing with the entry of angiosperms into Australia, and for the present study, a discussion of the factors which have led to diversity in the South West Province.

Knowledge of the Australian Angiosperm flora in the early Tertiary is considerably better than that of the earlier periods. The Eocene and Miocene are presumed to have been periods of adequate, reliable rainfall over southern Australia. This enabled the development of a so-called pan-Australian mesophytic flora which included *Cinnamomum*, *Nothofagus*, *Podocarpus*, *Casuarina*, *Banksia* and perhaps *Eucalyptus* (Crocker & Wood, 1947; Wood, 1959). In south-western Australia sediments of Eocene origin have revealed evidence of *Araucaria*, *Banksia*, *Nothofagus* and *Gleichenia* (McWhae *et al.*, 1958). From this evidence it is presumed that the climate of southern Australia was warm and wet. There is no evidence of climatic conditions in the mid-north of Western Australia, though warm water marine faunas are recorded during the Tertiary for the Carnarvon basin (Brown *et al.*, 1969). If the present climatic zones were applicable in the Miocene then it is possible that the area which is now North West Cape and the Hamersley Range experienced a Mediterranean type climate.

The Miocene period has been noted as an important one in Australian plant geography by Wood (1959). It marked the end of a long period of peneplanation, it was the beginning of earth movements in the south-east of the continent, and it was the beginning of the partial isolation of the South West Province from the rest of southern Australia.

In the Miocene to the Pliocene a marine transgression deposited the limestones which now constitute the Nullarbor Plain. This became an edaphic barrier between the east and west though, as will be suggested later, not a completely effective one.

Smith-White (*vide* Burbidge, 1960) suggests a pre-Miocene origin for many genera in the Rutaceae and Myrtaceae. It is likely that if this is the case, the diversification and development of endemism in the South West Province commenced in this period. Perhaps the Eocene transgression, which may have extended over much of the southern part of the Western Shield marked the beginning of the diversification. At this time the higher mountains and ranges along the south coast of Western Australia would have been islands and as such would have acted as refugia. It is in refugia such as these that much evolutionary change could occur, especially during the subsequent migration and intermingling of these refugial floras on newly liberated soils of the Oligocene and Miocene.

Another important factor contributing to the development of the flora in the Miocene was probably the development of laterite in the humid climate. Lateritization of the whole plateau commenced in the Eocene or Miocene but subsequent aridity restricted formation to the wetter south-west. The shield could have been colonised by laterite-tolerant species from the south or north-west to give a widespread flora adapted to the post-Miocene drier conditions. This flora was to a certain extent cut off from the eastern parts of the continent.

Later weathering of the laterites on the central part of the shield would have broken the continuous flora: two large remnants of these which exist today are the northern and southern sandplains, which have numerous disjunct species, i.e., only occurring in these regions or in isolated areas in between.

The scanty evidence of the post-Miocene floras has been discussed by Burbidge (1960). It is possible that the *Cinnamomum* type vegetation moved northward in response to a cooling of the climate leaving behind some of the present flora which had adapted to the changed conditions.

Specht and Rayson (1957) suggest that the present day sclerophyll genera developed in a warmer, wetter climate. The growth of these plants occurs at a time of great water stress in the late summer. This is interpreted as being out of phase with the present climatic conditions and a result of their origin in a more humid climate. It is possible that the leafy shoots which initiate and differentiate small, rigid cells in a period of stress would have an evolutionary advantage under arid conditions.

A number of authors, including Wood (1959), Smith-White (1954), Burbidge (1960) and Green (1964), stress the importance of the Miocene inundation and the subsequent development of limestone and arid land to the north, as a major barrier to plant migration between the east and west. Recent surveys of the area to the north of the Nullarbor Plains have revealed a surprising number of genera and species which are normally considered as southwestern. These include *Acacia leptopetala* Benth., *Daviesia ulicifolia* Andr., *Leptospermum roei* Benth. and species of *Micro-myrtus*, *Thryptomene* and *Logania*.

It is evident from the existence of pockets of southwestern flora at North West Cape (lat.

22°S, long. 114°E) and Roe Plains, especially at Twilight Cove (approx. lat. 32°S, long. 116°E) as well as others of southwestern species on granitic monadnocks as far east as Kalgoorlie, that the present day vegetation of the South West Province was of much greater extent in the past. Evidence for climatic fluctuations in the recent past (4000 to 3000 BC) have been provided by Churchill (1968). Under pluvial conditions it can be imagined that the area north of the Nullarbor Plain could provide an effective corridor between the southwest and southeastern Australia. The importance of this corridor for birds has been presented by Ford (1971).

Crocker and Wood (1947) postulated a mid-Recent period of aridity which, with subsequent amelioration of the climate causing contraction and expansion of the vegetation, had profound effect on the ecological and species complexity. During a period of severe southern Australian aridity the South West Province would have suffered greater decimation of the vegetation than the southeastern Australian region. The southeast in contrast to the west has a greater latitudinal and altitudinal variation. In the south-west three refugial areas could have been important. One of these is the Hamersley Range (approx. lat. 22°S, long. 118°W). The refugial nature of the present day Hamersley Range flora has been commented on by Burbidge (1959). If the arid period in southern Australia postulated by Crocker and Wood (*l.c.*) was due to a relative southwards movement of the weather zones in the mid-Recent as has been proposed by Keble (1947), Gentilli (1961) and Specht (1958), then it is likely that more of northern Australia came under the influence of monsoonal weather patterns. The Hamersley region could not only have provided a refugium for some southwestern species but also allowed some mixing of these with species of northern origin.

Two areas of refugial nature are postulated in the south-west. One is the deeper valleys of the Darling Scarp which because of uplift of rain-bearing westerly winds would always have a higher rainfall than the neighbouring plateau and coastal plain. From these refugia the recolonization of the laterites to the east of the scarp and the coastal plain could have taken place.

The remaining refugia could have been provided by the monadnocks and ranges, particularly along the south coast. These were probably the most important areas because of the variety of habitats available and the relative reliability of rainfall. If the mean path of the high pressure wind systems was much lower than at present, the on-shore winds would have brought more or less reliable rains to the south coast as they do in summer today. Such refugia as the Stirling Range and Barrens could have developed a species diversity and degree of endemism similar to that of the present Cape Peninsula.

The South West Province is not a centre of origin of the Australia flora but a centre of great diversity of some of these elements and of some relict groups. Continental drift occurred too early to have a profound effect on relationships with southern Africa. The diversity is

due to the long standing stability of the western plateau with diversity beginning in the Miocene and continuing with limited migration between east and west and north and south. The whole Southwestern corner of Australia developed into a virtual island which underwent drastic climatic change which must have favoured species adapted to sandy and gravelly soils. The South West Province can be regarded as a relatively isolated area with a latitudinal spread of only 9° and a limited altitudinal variation. This "island" has always been well away from any migration routes. Eastern Australia, in contrast to the south-west, has a latitudinal range of over 35° with a wide altitudinal variation. According to Burbidge (1960) this part of Australia is also a well developed migration route parallel and related to other routes from New Guinea to New Caledonia and New Zealand.

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